

**EFFECTS OF INCREASED DROUGHT AND SELECTIVE  
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COEXISTING MEDITERRANEAN OAKS WITH  
CONTRASTING LEAF HABIT  
(*Quercus ilex* and *Quercus cerrioides*)**



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TRABAJO DE INVESTIGACIÓN  
DOCTORADO EN CIENCIAS AMBIENTALES

**Effects of increased drought and selective thinning on growth and resprouting of  
two coexisting mediterranean oaks with contrasting leaf habit  
(*Quercus ilex* and *Quercus cerrioides*)**

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A mi familia y amigos, que desafían  
las leyes del espacio y el tiempo  
para estar siempre a mi lado a  
pesar de la distancia.

*El hombre no posee la Tierra. Sólo forma parte de  
ella. Lo que el Hombre le hace a la Tierra se lo  
hace a sí mismo...*

## **Agradecimientos**

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Por último, y ya en el plano personal, quiero dar las gracias a todas aquellas personas que durante estos dos años me han ayudado a mantener la moral alta en algunos momentos en que previsiblemente, de tener que afrontarlos sola, me habría derrumbado. Elaborar una lista me llevaría horas, ya que no se trata necesariamente de las personas con las que más tiempo he convivido, sino de aquellas que aparecieron por su propia voluntad en ciertos momentos clave en que no me hubiera atrevido a reclamar ayuda. A todas esas personas que me brindaron su apoyo incondicional en un momento en que yo no podía devolverles nada a cambio, a todas ellas no sólo tengo que darles las gracias, sino también decirles que las quiero.

Hay un pedacito de todos vosotros en este trabajo... y también dentro de mí. Mil gracias.  
Miriam

**Abstract**

According to the IPCC (2007), the Mediterranean basin is expected to suffer important changes in temperature and precipitation in the next few decades, leading the climate warmer and dryer. Therefore, it is necessary to determine the possible effects of increased drought on species with different structural and physiological traits, to be able to predict possible changes in the structure and composition of Mediterranean forests. Moreover, it will be necessary to assess whether traditional management practices can mitigate the effects of climate change on these forests. The main aim of this study has been to analyze the effects of increased drought on the mortality, growth and resprouting patterns of two co-occurring Mediterranean oak species with contrasting leaf habit (the evergreen *Quercus ilex* and the winter-deciduous *Quercus cerrioides*), and to assess the effects of selective thinning on their response to increased drought. Our results show a differential effect of increased drought between species: no differences were observed in the growth of *Q. ilex* while *Q. cerrioides* reduced its growth under increased drought conditions. Selective thinning reduced the negative effects of increased drought on tree growth, although this beneficial effect tended to decrease during the experiment. Our results show that increasing aridity in Mediterranean areas can be a constraining factor for deciduous oaks, thus potentially causing their decline in mixed forests and favouring their substitution by the evergreen congeneric species. However, as seen in this study, management can strongly encourage growth both for deciduous and evergreen species, thus reversing the effects of increased water stress on Mediterranean coppices.

**Key words:** Climate change, mixed oak coppices, drought, resprouting, *Quercus ilex*, *Quercus cerrioides*, thinning.

## Introduction

Mediterranean regions are expected to be one of the most vulnerable areas in the world to climate change (IPCC 2007). Over the last century, temperatures have already shown an overall trend towards warming in the Mediterranean basin (Piñol et al 1998; Peñuelas et al 2002). This situation may turn out to be even more drastic under the new conditions predicted for the current century. On its report of 2007, the IPCC predicts for this region an increase in mean temperature between 2.2 to 5.1 °C. Concerning precipitation, the forecasted changes are more ambiguous, with a potential reduction of 4-27% of rainfall. The maintenance of the current precipitation values or their decrease, coupled with enhanced evapotranspiration in spring and early summer due to warming, is very likely to lead to reduced summer soil moisture and recurrent drought episodes in the Mediterranean areas (Douville 2002; Wang 2005).

Since water stress is already the main constraining factor in Mediterranean forests (Spetch 1988), a decrease in water availability is likely to affect their productivity and their resilience after disturbances (Peñuelas 1996). Indeed, an increase in water deficit could induce ecophysiological changes in different species affecting their growth and survival (Tenhunnen et al 1990; Filella et al 1998) and, in the long-term, their distribution and abundance (Gucci et al 1999; Ogaya and Peñuelas 2007a). The response of plants to water stress depends on their structural and physiological traits. Thus, the effects of increased drought may vary between the different species, as it has been suggested by experimental and modeling studies (Martinez-Vilalta et al 2002; Sabaté et al 2002; Ogaya et al 2003; Lloret et al 2004; Ogaya and Peñuelas 2007a,2007b). In light of the potential species-specific effects of climate change, leaf lifespan could be an important factor influencing the survival and growth of the different species subjected to increased drought. It has been argued that evergreen habit can be an advantage in water poor habitats due to its low resources-losses ratios

(Berendse 1994; Aerts 1995) in comparison to the higher levels of water availability required by deciduous species (Villar et al. 1995; Eamus 1999; Villar and Merino 2001; Quero et al 2006). In contrast with the abundance of studies aimed to evaluate the potential effects of climate change in the structure and functioning of Mediterranean forests and the existence of species-specific responses, very few have addressed whether forest management can mitigate the consequences of increased drought. Yet, the potential importance of management practices to reduce the impact of climate change has been often suggested (see Bravo-Oviedo 2006, eds).

In the Mediterranean basin, where the co-occurrence of evergreen and winter-deciduous species is usual, mixed oaks forests with contrasting leaf habit are relatively abundant (Johnson et al 2002; Quezel and Medail 2003). Due to traditional management practices and the recurrence of disturbances (e.g. wildfires, overgrazing) most Mediterranean oak forests are “coppices” characterised by high-density stands of multi-stemmed stools with relatively small resprouts, slow vertical growth and low production rates (Cañellas et al 1996 ; Terradas 1999; Espelta et al 2003). In this kind of forests, the high water competition within stools reduces the amount of water available for every stem (Cuttini and Benvenuti 1996; Gracia et al 1999). To ameliorate the structure of these forests and encourage their sexual regeneration, it has been suggested their mid-term gradual conversion into “stored coppices” (i.e. coppices in which there remains only one or two stems per stool) or in the long-term to “high forests”, through the selection and elimination of the weakest resprouts (Serrada et al 1996). This process could increase the availability of resources such as water and nutrients for the remaining stems through reducing competition among the stools (Ducrey and Toth 1992; Serrada and Bravo 1997).

There are several studies documenting the response of Mediterranean oaks to water stress in terms of survival and growth (Mayor and Roda 1994; Lloret et al 2004; Koch



et al 2004; Ogaya et al 2003; Ogaya and Peñuelas 2007a), as well as the effects of thinning on growth and resprouting (Ducrey and Toth 1992; Retana et al 1992; Cutini and Mascia 1996; Serrada et al 1996; Serrada and Bravo 1997; Espelta et al 2003). Notwithstanding, there is a lack of information about the combination of these two factors on different species with contrasting leaf habit. This information may be a key factor to manage mixed Mediterranean oak forests in the context of global change.

The main aim of the present study has been to analyze the effects of increased drought on the mortality, growth and resprouting patterns of two co-occurring Mediterranean oak species with contrasting leaf habit (the evergreen *Q. ilex* and the winter-deciduous *Q. cerrrioides*), and the potential effects of forest management (selective thinning) on their response to increased drought. To achieve these objectives we have carried out an experiment during two consecutive years (from 2005 to 2007) in a mixed oak forest where we have applied two levels of water stress and we have carried out two levels of forest management. The results obtained in this study may improve our knowledge about the response of different Mediterranean species to the new climatic constraints predicted for the next decades as well as to develop management practices to mitigate the effects of climate change on Mediterranean forests.

## Material and methods

### Study area

The research was conducted in a forested area in the region of Bages, Catalonia, NE Spain (41° 44'N, 1°39'E), from January 2005 to February 2007. The mean elevation in the study site is 800 m, with south aspect and slope of about 10%. According to the data provided by the Meteorological Service of Catalonia, mean annual temperature is 12°C, with an oscillation between 4°C in January and 22°C in July. Mean precipitation, characterized by its irregular distribution among the year and its high year-to-year fluctuation in timing and amount, is 600 mm. The climate, according to Thornwaite index, is dry-subhumid Mediterranean, with dry and warm summers, moderate cold winters and irregular precipitation distributed mainly during the autumn season. The geological substrate is predominantly calcareous, surface rockiness is high and soil is moderately well drained with a mean depth c.a. 25-50 cm (M. Cotillas, personal observation).



**Figure 1.** The study area and the wildfire boundary in winter (left) and spring (right) 2007. From the wildfire border to the left, we can see a mixed oak forest in regeneration. At the right, a forest of *Pinus nigra* which survived to the fire.

The site was affected by a large wildfire in 1998, which burned about 15,300 ha of forested area. According to the data provided by the Ecological Forest Inventory of

Catalonia (IEFC) (Gracia et al 2000) before the fire the study area was covered by black pine (*Pinus nigra*) forests, with the oaks *Quercus ilex* and *Quercus cerrioides* extensively present in the understory. A failure in the regeneration of *P.nigra* (see Espelta et al 2002) led most of these burned areas into mixed forests of *Q.ilex* and *Q.cerrioides* (**Figure 1**), regenerated by resprouting and forming a typical structure of a coppice with numerous multi-stemmed stools (Espelta et al 2003). These are typical Mediterranean oaks and can form either monospecific or mixed forests (Terradas 1999). They share in common some life-history traits, but differ markedly in their leaf habit. *Q.ilex* is a typical sclerophyllous evergreen oak, while *Q.cerrioides* is a winter-deciduous oak.

### **Experimental design and sampling**

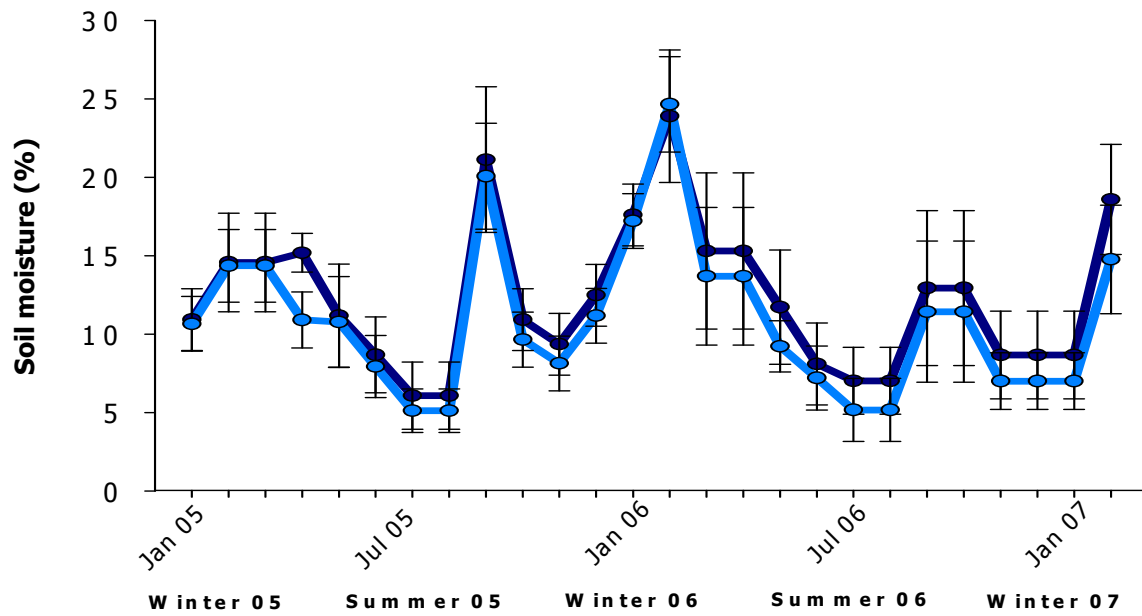
In order to test for the effects of an increase in water stress and forest management on the survival, growth and resprouting patterns of mixed forests of *Q.ilex* and *Q.cerrioides*, we conducted an experiment between 2005 and 2007 in a sampling area of 10.8 ha in the previously described forest.



**Figure 2.** The rain exclusion device

Following a factorial design, two levels of water stress (natural drought and increased drought) and management (thinning and no thinning) were combined in four treatments, with 3 replicates (plots) each. The 12 plots (15m x 20m) were randomly distributed in the sampling area. Increased drought simulation was done through the installation of parallel drainage channels covering 15% of ground surface on the selected plots (**Figure 2**). This device was aimed to capture around 15% of rainfall, which, according to the IPCC (2001) and other Global Climate Models, was the predicted decline in precipitation for this area in the next decades. Soil moisture was

monitored through Time Domain Reflectometer (TDR) probes in ten points for each plot. The sampling of TDR probes was carried out during two weeks for every season with some intermediate sampling days since the onset of the experiment. The pattern of soil moisture in the natural-drought and increased-drought plots is shown in **Figure 3**.



**Figure 3.** Dynamics in soil moisture during the experiment (mean  $\pm$  SE)

Mean reduction of soil moisture in increased-drought plots was 10%, varying between 0% and 20%. Along the two years monitored the accumulated percentage of soil moisture reduction in increased drought plots was 770 %. Selective thinning was done by hand, leaving from one to up to three stems per stool, generally the highest ones.



**Figure 4.** General appearance of a non-thinned plot (left) and a thinned one (right).

To evaluate the changes induced by the experimental treatments, basal diameter and height were measured for all stems within each plot, at the onset of the experiment and every year during the study (2005, 2006 and 2007). Due to the particular structure of oak coppices (multi-stemmed stools) we calculated both the individual stem basal area and the total stool basal area (s.e. the sum of the basal areas of all stems per stool). The stem basal area can be an appropriate measure of stem growth while total stool basal area gives a more detailed view of the dynamics at the individual level and total biomass accumulation. To avoid pseudoreplication, stem basal area and height were calculated as mean values per stool. Mean values of all parameters were calculated every year for every plot and for every species, to be used as the variables in the following analysis.

In those plots subjected to thinning, a new wave of basal resprouts appeared by 2005, one year after the management practices. The total amount of new resprouts per stool, as well as their mean height, was also measured every year during the experiment.

### **Data analysis**

At the onset of the experiment, a three-way ANCOVA was performed to analyse the effect of the assigned treatment and the species (*Q.cerrioides* and *Q.ilex*) on the initial stool basal area, stem basal area and stem height, as well as the total amount and the mean height of the new resprouts in the thinned plots. In this analysis we included as a covariate the initial density of the stools due to the different number of stools among plots. The effects of the experimental treatments on these variables at the initial stage of the experiment are summarized in **table 1**.

At the initial stage, *Q.cerrioides* and *Q.ilex* showed significant differences for all the structural characteristics related to their resprouting pattern. *Q.cerrioides* individuals

had larger stem basal area ( $1237 \pm 79 \text{ mm}^2$ ) and longer height ( $177 \pm 4 \text{ cm}$ ) than those of *Q.ilex* ( $967 \pm 79 \text{ mm}^2$  and  $144 \pm 4 \text{ cm}$ , respectively). Furthermore, *Q.cerrioides* stools in the thinned plots presented a lower number of new resprouts than *Q.ilex* ones ( $11 \pm 2$  vs.  $19 \pm 2$  resprouts, respectively). Management had also an important effect on the initial conditions, since it involved a selection of the largest resprouts and the suppression of the weakest ones in the plots subjected to thinning. This implied a larger initial stem basal area ( $1433 \pm 81 \text{ mm}^2$  vs.  $770 \pm 81 \text{ mm}^2$ ) and stem height ( $175 \pm 4 \text{ cm}$  vs.  $146 \pm 4 \text{ cm}$ ) in those plots. Conversely, total stool basal area was lower in managed plots ( $2142 \pm 232 \text{ mm}^2$ ) than in non-managed ones ( $3318 \pm 237 \text{ mm}^2$ ) because thinning had eliminated between 20% and 30% of the total basal area per stool in managed plots. An interaction between management and species indicates that in non-thinned plots, *Q.cerrioides* had a larger initial stool basal area than *Q.ilex* ( $3816 \pm 324 \text{ mm}^2$  vs.  $2820 \pm 324 \text{ mm}^2$ ), while the opposite happened in thinned plots ( $1954 \pm 324 \text{ mm}^2$  vs.  $2331 \pm 324 \text{ mm}^2$ ). Concerning water stress, no effects were found between the assigned treatment and the initial basal area of stems or stools, the height of stems or the amount or mean height of the new resprouts at this stage.

	Initial measures in 2005			New resprouting in 2005	
	Stem basal area	Stool basal area	Stem height	Total amount of new resprouts	Mean height
Stand density	<b>11,320**</b>	<b>9,480**</b>	<b>25,338***</b>	<b>3,872**</b>	<b>4,536<sup>o</sup></b>
Water stress	0,001	0,043	0,081	0,275	1,968
Management	<b>32,210***</b>	<b>12,334**</b>	<b>20,350***</b>		
Species	<b>5,821*</b>	0,931	<b>27,718***</b>	1,022	1,321
Water stress * Management	0,363	0,002	0,404		
Water stress * Species	0,275	0,045	0,006		
Management * Species	0,094	<b>4,590*</b>	1,963		

**Table 1.** F-values for all variables at the onset of the experiment <sup>o</sup>p<0.1; \*p<0.05; \*\*p<0.001;\*\*\*p<0.001

Because of the initial differences between species and management levels, we employed relative growth rate instead of absolute growth as the variable for the analysis. Relative growth rate (RGR) was calculated as

$$RGR_{x_i - x_{i-1}} = \frac{x_i - x_{i-1}}{x_{i-1}} \times 100$$

where  $X_i$  was the value of the selected variable in year  $i$ , and  $X_{i-1}$  was its value in the previous year.

Relative growth rate in stem basal area, stool basal area and height were analysed through a repeated-measures three-way ANCOVA model. Management (thinned vs. non-thinned), water stress (natural stress drought vs. increased drought) and species (*Q.ilex* and *Q.cerrioides*) were included as within-subject factors, year (2005, 2006) as a between-subject factor and stand density as a covariate.

The number of new resprouts and their mean height were analysed through a repeated-measures two-way ANCOVA, where water stress and species were included as within-subject factors, year as a between-subject factor, and stand density as a covariate. Management treatment was not included in the model because new resprouting only took place in those plots subjected to thinning.

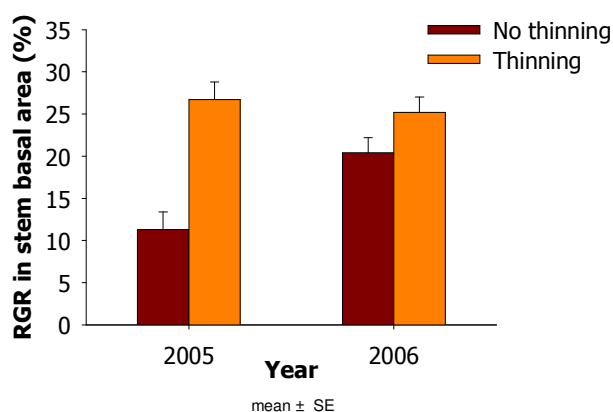
## Results

The two different levels of water stress (natural drought vs. increased drought) did not affect the survival of stems (**Table 2**). Conversely, thinning was a very important factor to reduce stem mortality (**Table 2**), since mortality was much lower in thinned plots compared to non-thinned ones ( $5 \pm 0.7 \%$  vs.  $26 \pm 0.7 \%$ , respectively). Management did also influence growth in basal area both at the stem and at the stool level (**Table 3**). Thinning enhanced relative growth rate in stem basal area ( $26.0 \pm 1.4 \%$  in thinned plots vs.  $15.8 \pm 1.4 \%$  in non-thinned ones) and in stool basal area ( $25.8 \pm 2.0 \%$  vs.  $17.0 \pm 2.0 \%$ ). However, the interaction between management and year (**Table 3**) points out that the encouraging effect of thinning on growth in basal area decreased in 2006 respect to 2005 (**Figure 5** for stem basal area and **Figure 6** for stool basal area). Concerning water stress, a significant effect was observed on the growth in basal area of stems (interaction water stress x management x year in **Table 3**). As shown in **Figure 7**, in 2005 the growth in stem basal area was similar in plots subjected to natural and increased drought and it was only ameliorated in those plots where selective thinning was applied. Conversely, in 2006, increased drought reduced the growth in non-thinned plots but not in the thinned ones. This means that in the second year of the experiment thinning mitigated the negative effects of increased drought for growth in stem basal area, so individuals growing under increased drought conditions could reach similar growth values than those subjected to natural drought. Concerning the two oak species, no differences were observed for the relative growth in basal area. Therefore at the end of the experiment (2007) the initial differences between *Q. cerrioides* and *Q. ilex* persisted (**table 4**): *Q. cerrioides* had a larger stem basal area than *Q. ilex* ( $1662 \pm 98 \text{ mm}^2$  vs.  $1370 \pm 98 \text{ mm}^2$ , respectively). For stool basal area, *Q. cerrioides* had a larger basal area than *Q. ilex* by 2007 in non-thinned plots, while the opposite trend was observed in thinned ones (**Figure 8**).

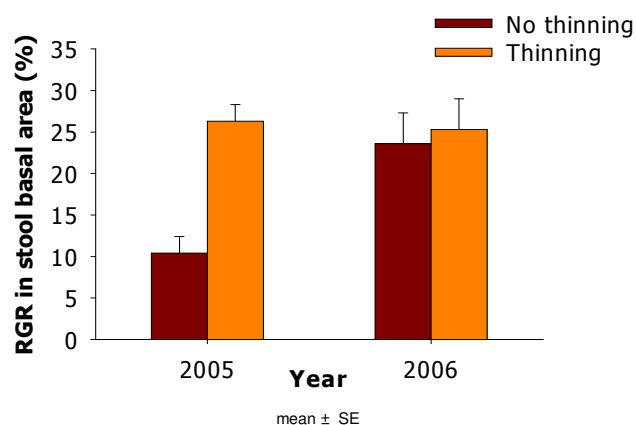


	<i>Mortality</i>
Stand density	3,026
Water stress	0,167
Management	<b>4,569*</b>
Species	0,592
Water stress * Management	0,090
Water stress * Species	0,360
Management * Species	1,514

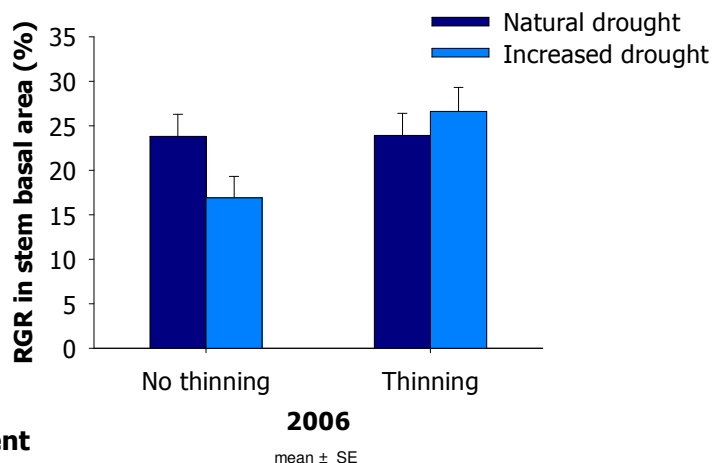
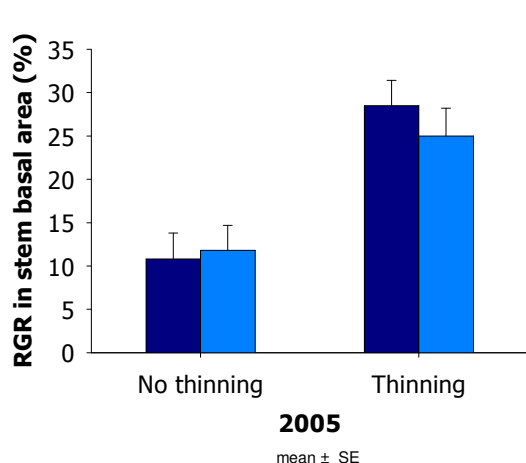
**Table 2.** Interaction F-values for mortality. <sup>a</sup>p<0.1; \*p<0.05; \*\*p<0.01;\*\*\*p<0.001



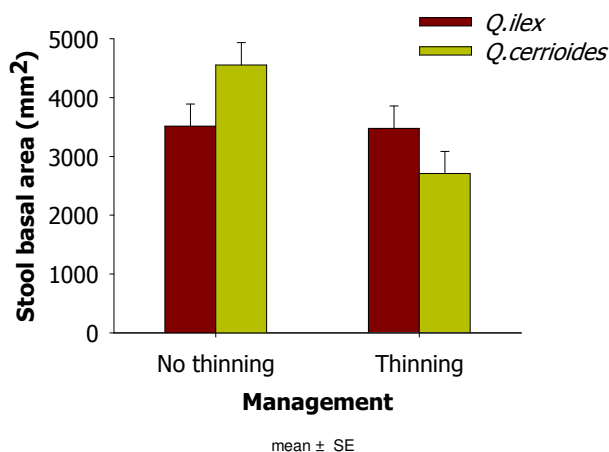
**Figure 5.** Interaction Management x Year for RGR in stem basal area



**Figure 6.** Interaction management x year for RGR in stool basal area.



**Figure 7.** Interaction Year x Water stress x Management for RGR in stem basal area.



**Figure 8.** Interaction Species x Management for stool basal area by 2007.

As previously shown for basal area, the experimental treatments did also modify the patterns of height growth (**Table 3**). Plots subjected to thinning presented a significantly higher relative growth in height than non-thinned ones ( $6.4 \pm 0.3$  % vs.  $4.1 \pm 0.3$  %, respectively). Notwithstanding, the interaction management x year (**Table 3**) indicates that the encouraging effect of thinning decreased during the second year of the experiment (**Figure 9**). As for basal area, water stress influenced height growth (**Table 3**). Interestingly, the effects of increased drought were different in the two oak species: increased drought barely modified the height growth of *Q. ilex* while it reduced that of *Q. cerrrioides* (**Figure 10**). Concerning the potential benefits of thinning to reduce the effects of drought in growth, the interaction management x water stress (**Table 3**) indicates that in absence of thinning, oaks presented low and similar growth rates irrespectively of the water stress conditions, while thinning increased growth rates both in natural-drought conditions and, to a lessen extent, in increased-drought plots (**Figure 11**). At the end of the experiment (**table 4**), mean height was higher in plots subjected to thinning than in control ones ( $195 \pm 5$  cm vs.  $157 \pm 5$  cm) and it was higher for *Q. cerrrioides* ( $193.26 \pm 4.81$  cm) than for *Q. ilex* ( $159.44 \pm 4.81$  cm).

	<i>Relative Growht Rate</i>		
	<i>Stem basal area</i>	<i>Stool basal area</i>	<i>Height</i>
Stand density	0,633	0,463	<b>9,803**</b>
Water stress	0,605	1,085	<b>5,024*</b>
Management	<b>24,357***</b>	<b>9,073**</b>	<b>39,201***</b>
Species	0,590	0,011	<b>3,315<sup>a</sup></b>
Water stress * Management	0,411	0,804	<b>4,534*</b>
Water stress * Species	0,004	0,162	<b>6,674*</b>
Management * Species	2,336	0,213	1,036
Year	0,237	0,204	0,004
Year * Stand density	0,011	0,007	0,815
Year * Water stress	0,051	0,445	1,760
Year * Management	<b>7,856*</b>	<b>5,072*</b>	<b>3,775<sup>a</sup></b>
Year * Species	2,727	0,080	0,001
Year * Water stress * Management	<b>3,664<sup>a</sup></b>	2,659	<b>3,234<sup>a</sup></b>
Year * Water stress * Specie	0,560	0,048	<b>3,045<sup>a</sup></b>
Year * Management * Species	1,053	1,392	1,288

**Table 3.** F-values for RGR in basal area and height. <sup>a</sup>p<0.1; \*p<0.05variables; \*\*p<0.01; \*\*\*p<0.001

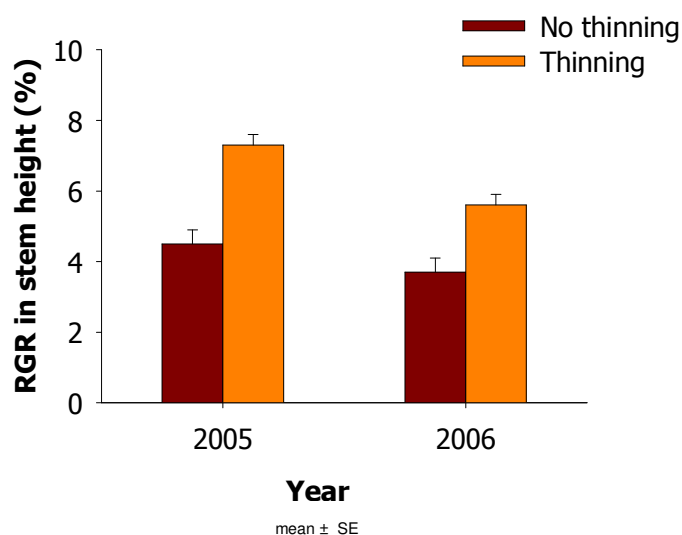


Figure 9. Interaction Water availability x Year for RGR in stem height.

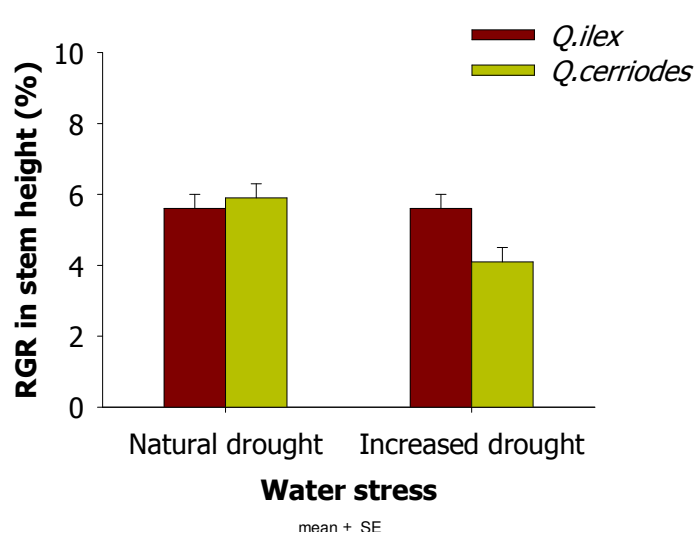


Figure 10. Interaction Species x Water stress for RGR in stem height.

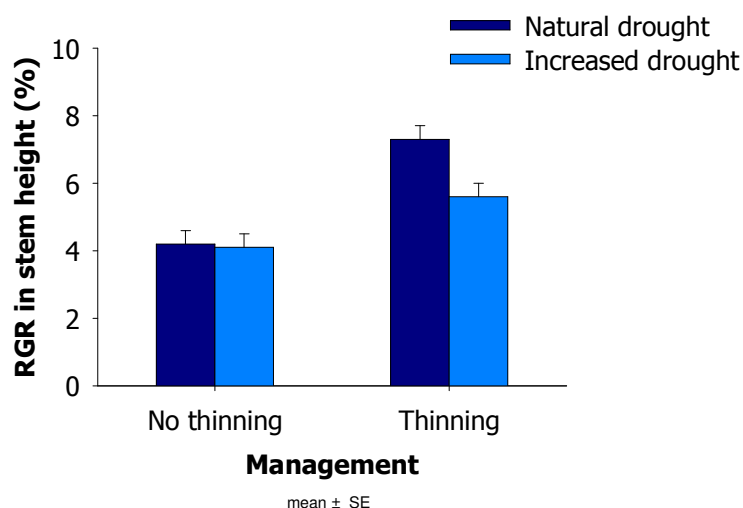
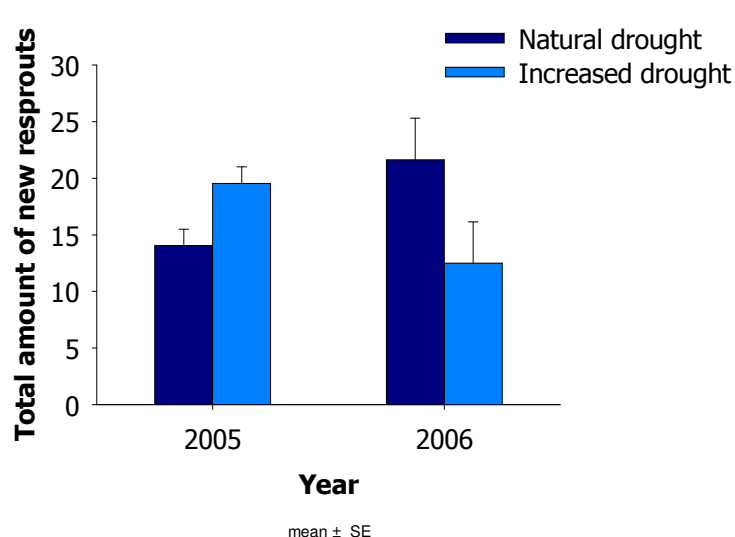


Figure 11. Interaction Water stress x Management for RGR in stem height.

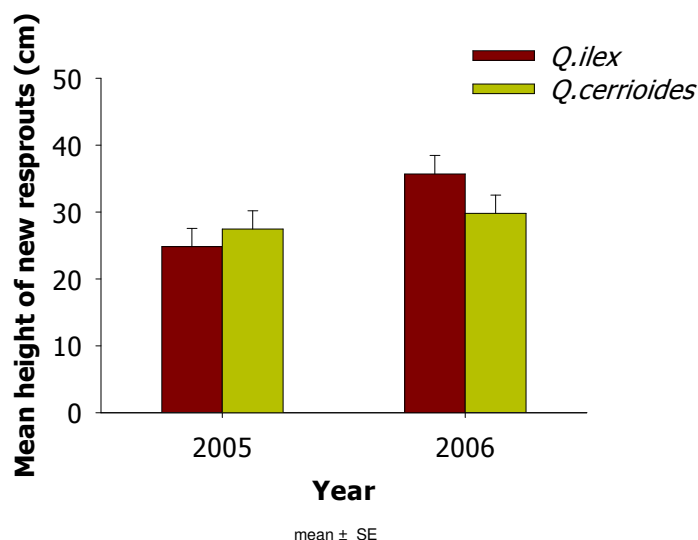
	Final measures in 2007			New resprouting in 2007	
	Stem basal area	Stool basal area	Height	Total amount of new resprouts	Mean height
Stand density	13,723**	11,462**	21,204***	2,185	3,616 <sup>a</sup>
Water stress	0,004	0,015	0,006	0,347	1,021
Management	59,926***	5,782*	30,170***		
Species	4,422 <sup>a</sup>	0,133	24,689***	2,019	2,315
Water stress * Management	0,229	0,000	0,033		
Water stress * Species	0,384	0,037	0,117		
Management * Species	0,030	5,843*	1,857		

Table 4: F-values for RGR in basal area and height. <sup>a</sup>p<0.1; \*p<0.05variables; \*\*p<0.01; \*\*\*p<0.001

Both *Q. ilex* and *Q. cerrioides* resprouted vigorously after the thinning treatment, with a significant effect of water stress on the resprouting dynamics (**Table 4**). The interaction year x water stress indicates that in 2005 oaks subjected to increased drought produced a higher number of new resprouts than those growing under natural drought conditions, while for 2006 the opposite trend was observed (**Figure 12**). The total number of new resprouts appeared during the experiment was higher for *Q. ilex* than for *Q. cerrioides* ( $21 \pm 2$  vs.  $13 \pm 2$ ). Moreover, the interaction year x species for the mean height of the new resprouts (**Table 4**) indicated that resprouts of *Q. ilex* grew more than those of *Q. cerrioides* in 2006 (**Figure 13**).



**Figure 12.** Interaction Water stress x Year in the total amount of new resprouts in thinned plots.



**Figure 13.** Interaction Species x Year for mean height of new resprouts in thinned plots

	New resprouting		
	Number of resprouts	Maximum height	Mean height
Stand density	0,083	2,420	<b>3,707<sup>a</sup></b>
Water stress	0,312	0,178	0,175
Species	<b>7,000*</b>	0,225	0,219
Year	0,036	0,027	1,328
Year * Stand density	0,048	0,685	0,152
Year * Water stress	<b>9,109*</b>	0,530	1,927
Year * Species	0,012	<b>21,833**</b>	<b>5,794*</b>

**Table 4.** Interaction F-values for new resprouting variables. <sup>a</sup>p<0.1; \*p<0.05; \*\*p<0.01; \*\*\*p<0.001

## Discussion

The rainfall exclusion treatment (s.e. increased drought) resulted in highly heterogeneous effects on soil moisture, since the differences between plots under natural drought and those subjected to increased drought oscillated between 0% and 20% depending on the season of the year, according to the TDR probes. Nevertheless, these differences seem to progressively enlarge with time, probably reflecting some accumulative effects on soil moisture (**Figure 3**).

Increased drought did not modify *Q. ilex* and *Q. cerrioides* survival, probably because the level of water stress was much lower than that experienced under severe drought episodes, when mortality of oaks has been recorded (Lloret and Siscart 2004). Conversely, management was an important factor encouraging survival in plots subjected to thinning (see also, Gracia et al 1999). It has been suggested that the reduction of competition between stems leads to increase water availability for the reserved stems, thus releasing the effects of water stress and its consequences (Amorini et al 1996; Cutini and Mascia 1996; Gracia et al 1999).

Despite the highly heterogeneous differences in soil moisture, increased drought had important effects on growth in height of *Q. cerrioides*, while no significant effect was observed for *Q. ilex* (but see, Ogaya and Peñuelas 2003, 2007a). This different sensitivity of stem growth to water stress for both oaks may be due to their different leaf habit, which can condition their physiological response to drought. It has been suggested that the ability of sclerophyllous oaks to avoid water stress is strongly dependent on increasing leaf hardening (Save et al 1999). Sclerophyllous-evergreen oaks have lower water losses and thus can maintain higher values of leafiness even under intense radiation (Damesin et al 1998; Espelta et al 2005), which can represent an advantage in water poor habitats. Conversely, deciduous oaks have higher specific

leaf area (Damesin et al 1998; Espelta et al 2005; Quero et al 2006), higher area-based photosynthetic and respiration rates, higher stomatal conductance and leaf nitrogen concentration (Villar et al 1995; Reich et al 1999; Villar and Merino 2001; Takashima et al 2004; Wright et al 2004, 2005) but lower leafiness than evergreen ones (Espelta et al 2005). Moreover, other studies have suggested that sustaining relatively short-lived, metabolically more active leaves in deciduous oaks requires a more efficient xylem compared to the long-lived, metabolically more conservative leaves of sclerophyllous-evergreen species (Kolb and Davis 1994). This would allow a greater efficiency in hydraulic transport by the xylem of deciduous stems that might permit higher transpiration rates during spring months, thus facilitating higher rates of photosynthesis (Tognetti et al 1998). These traits can let deciduous species reach higher relative growth rates than the evergreen congeneric ones (Antunez et al 2001; Ruiz-Roblero and Villar 2005), but makes their growth more dependent on water and nutrient availability, and thus more vulnerable to drought (Quero et al 2006, but see Schulze et al 1982, Espelta et al 2005). In a comparison of evergreen and deciduous Mediterranean oaks, Damesin et al (1998) found that although the leaf lifespan and the structure of *Q.ilex* and *Q.pubescens* differed, their functional characteristics related to carbon and water relations were very similar, and drought constraints were more likely to affect deciduous oaks via cavitation than because of their leaf physiological traits.

Selective thinning was an important factor encouraging growth in basal area and height (see also, Mayor and Roda 1993; Amorini et al 1998; Gracia et al 1999; Espelta et al 2003). Thinning has been argued to reduce competition for light, water and nutrients within the reserved stems, which allows them to reach higher growth rates in comparison to non-thinned stools (Ducrey y Toth 1992; Cuttini and Mascia 1996). Interestingly, our results show that thinning could partially mitigate the effects of increased drought. For basal area, increased drought reduced growth in non-thinned plots in 2006, while thinned ones showed a higher growth independently of the water

stress. This indicates the release power of thinning under increased drought conditions. Conversely, for basal area in 2005 and height within both years, growth rates in non-thinned plots were very low independently of the water stress, while in thinned plots growth rates became much higher, with a lower rate in plots subjected to increased drought (**Figure 7** and **Figure 11**). Considering that according to the meteorological data for this area winter and spring 2005 were especially dry, these results may indicate that in absence of management Mediterranean oak coppices are already so constrained by water stress that a 15% of decrease in rainfall does not have any additional effect on stem growth, especially in drier years. The effects of management on growth in basal area and height decrease with time, being more important in 2005 than in 2006. Similar results have been obtained in other studies (Mayor and Roda 1993; Espelta et al 2003), and our hypothesis is that this decrease in growth rates with time is due to the production a new flush of basal resprouts that compete with the reserved stems for water and nutrients.

Increased drought seems to initially encourage the production of new resprouts in thinned oaks, since in 2005 the total number of new resprouts produced was higher in plots subjected to increased drought. However, this tendency reversed in 2006. This can be due to the induction by water stress of the activation of dormant buds in the root collar (Champagnat 1989), but the later survival of a fewer number of resprouts. The total number of new resprouts, as well as their maximum or mean height was higher for *Q. ilex* than for *Q.cerrioides*, which accord with the results found in previous studies (Espelta et al., 2003) and can represent an advantage of *Q.ilex* to face recurrent disturbances (Lloret and López Soria 1993; Espelta et al 1999), in spite of the negative effects that this effort of new resprouting can cause over the growth rates of this species (Vigneron 1988; Bergez et al 1990).

By the end of the experiment (**table 4**), managed plots had a higher stem basal area and height than unmanaged ones, and *Q.cerrioides* had a larger shoot basal area and height than *Q.ilex*. This confirms the higher resprouting vigour of the former species (Espelta et al 2003) and maybe due to the higher inversion of resources in *Q.ilex* in a new resprouting wave. However, for stool basal area *Q.ilex* was not affected by management, since it attained in two years the same basal area in thinned plots than in non-thinned ones, while the stool basal area of *Q.cerrioides* remained smaller in thinned plots. This indicates that the recover of lost basal area after a perturbation is faster for *Q. ilex* than for *Q. cerrioides*.

The preliminary results obtained in this experiment may be important in light of the forecasted scenario of climate change in Mediterranean oak forests. According to our results increasing aridity in Mediterranean areas can be a constraining factor for the growth of deciduous oaks, thus causing their potential decline in mixed forests and favouring their substitution by the evergreen congeneric ones. However, our results show that management can strongly encourage growth both for deciduous and evergreen species, thus reversing the effects of increasing water stress on Mediterranean coppices. Therefore, thinning appears as an interesting alternative to manage forests constrained by drought, improving their growth and survival in a predicted scenario of climate change.



## Conclusions

1- A slight decrease in rainfall had important effects on mixed oak forests of *Q.ilex* and *Q.cerrioides*. It did not affect the growth of the evergreen *Q.ilex*, while the growth in height of the deciduous *Q.cerrioides* decreased considerably under increased drought conditions. This can indicate a higher vulnerability to drought of deciduous Mediterranean oaks compared to evergreen ones.

2- Thinning had important effects reducing mortality and enhancing growth, both for basal area and height. Moreover, it can also mitigate the effects of increased drought. In 2006 (the wettest year) stem growth in basal area in non-thinned plots was lower under increased drought conditions, while when thinned, stems reached the same rates as those growing under natural drought. This indicates a releasing effect of thinning of drought effects. Conversely, for basal area in 2005 (with exceptionally dry conditions in winter and spring) and for height within both years, growth rates in non-thinned plots were very low independently of the water stress. In thinned plots, on the contrary, growth was much higher, with lower rates in plots suffering increased drought. Our hypothesis is that non-managed mixed coppices are already so constrained by water stress that a reduction of 15% in rainfall does not have additional effects on their current low growth rates in height or in basal area in the drier years.

3- The total amount of new resprouts was higher in plots suffering additional drought in 2005, while this difference disappeared in 2006. This can be due to the activation of dormant buds in the root collar due to water stress.

4- These results highlight that thinning can be an important factor encouraging growth and survival under increased drought conditions, thus been able to modify some of the predicted effects of climate change in Mediterranean mixed oak coppices.

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